THE INNERVATION OF THE HEART OF THE ELASMOBRANCH, *SCYLLIUM CANICULA*

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The elasmobranch fishes have certain features, both structural and physiological, which make them of interest from a comparative viewpoint. The well developed cranial parasympathetic system and the poorly developed sympathetic pointed out by Müller and Liljestrand (1918), the abundant chromaphil tissue quite separate from the interrenal tissue first described by Balfour (1878), the extraordinarily high urea content of the blood, the significance of which Baglioni (1906) has studied, the marked cardiac and respiratory inhibition and the absence of vaso-motor responses noted by Schoenlein and Willem (1894) and the inhibitory action of adrenaline on the heart first noted by Macdonald (1925) are some examples. An attempt, however, to find a detailed description of the vagus supply to the heart of *Scyllium canicula*, which has been the chief type used, was unsuccessful, although the course of the vagus in certain fishes has been described by Dogiel and Archangelsky (1906). In the pike (*Esox lucino*) these authors trace a ramus cardiacus from the visceral trunk to the sinus-auricle junction where a plexus is formed giving off fibers to the ventricle. In *Scyllium*, Marshall and Hurst (1905) state that the visceral branch of the vagus gives off cardiac nerves to the heart. In the dogfish, *Squalus acanthias*, Norris and Hughes (1920) describe the cardiac ramus as arising from the post-branchial branch of the fourth branchial division of the vagus (fifth branchial nerve). In an investigation of the cardio-inhibitory reflex and of the visceral afferent nervous pathway in *Scyllium* the writer found it necessary to examine the vagus supply to the heart in some detail. Incidentally some observations were made on the presence of vagal tone.

Bottazzi (1902) attempted to demonstrate an accelerator innervation of the heart of *Scyllium*, with the medulla separated from the spinal cord, by stimulating various sections of the cord and the first sympathetic ganglion, but obtained no acceleration in the rate. With the idea that possibly there were accelerator fibers entering with the vagus, he stimulated this nerve electrically with gradually increasing

strengths of stimulus, but got only inhibition. He did not perfuse the gills during the procedure. Müller and Liljestrand (1918), in a morphological study, could find no nerve fibers running to the heart from the first large sympathetic ganglion in elasmobranchs. Since Zwaardemaker (1925) claims to have found cardio-accelerator nerves in *Petromyzon* in which previously both Greene (1902) and Carlson (1904) had failed to demonstrate such nerves, the writer considered it worth while to repeat, with perfusion of the gills, Bottazzi's experiments, and to try certain other procedures which might possibly reveal the presence of an accelerator control of the heart.

Material and Methods

Specimens of *Scyllium canicula* averaging 300 grams were used. Gross dissections were made in living fishes with the brain destroyed anterior to the optic lobes and the spinal cord pithed posteriorly from various levels. Morphological observations were checked by stimulating the nerves in question both centrally and peripherally with a faradic current, or by cutting all nerves except the one to be examined and testing its function in reflex cardio-inhibition. In one case a complete dissection was stained with osmic acid. By a method described in a previous paper (Lutz, 1930) the heart and the respiratory rate were recorded.

A similar type of preparation, with certain parts of the nervous system destroyed and with the gills perfused, was used to investigate the possible existence of accelerator influence.

Results

In studying reflex cardio-inhibition it was at once obvious that cutting the cardiac root of the visceral branch of both vagi failed to prevent reflex cardiac arrest on stimulation of the skin and various other points. On the assumption that *Scyllium* might be similar to *Squalus* with respect to vagus innervation, the post-branchial root of the fourth branchial division (fifth branchial nerve) on each side was also cut. This procedure prevented the elicitation of reflex cardio-inhibition. Cutting either pair of roots alone did not prevent direct inhibition of the heart on stimulation of the nerve anterior to the fourth branchial division. All four nerves must be cut, or section of the main trunk be made anterior to the fourth branchial division in order to remove all vagus influence. A careful dissection was then made of many specimens and the two branches from each vagus were found to run to the Cuverian duct and there anastomose on the wall of this large

vein before passing to the heart. Weak faradic stimulation of the cut distal portion of each branch produced inhibition, and stimulation of the central end caused reflex cardio-inhibition provided any one of the branches remained intact.

Reflex cardiac and respiratory inhibition was obtained on mechanical stimulation of the dorsal surface of the ventricle either by pinching it lightly with the fine forceps or by sticking the epicardium with a sharp needle (Fig. 1, *A* and *B*). This was also obtained after the aorta had been transected. Reflex cardio-inhibition was also elicited on weak faradic stimulation of the ventricle in a fish with the spinal cord pithed posteriorly from the fifth vertebra and the hypobranchial nerve and all other spinal nerves of the region cut. All branches of the vagus except the post-branchial ramus of the fourth branchial division on each side were cut (Fig. 1, *C*). The cardio-inhibition was accompanied by

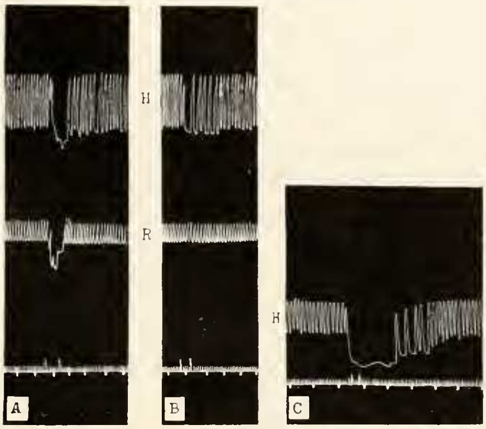

FIG. 1. Reflex cardiac and respiratory inhibition on stimulation of the dorsal surface of the ventricle of *Scyllium canicula* with the forebrain destroyed and the spinal cord pithed posteriorly from the fifth vertebra. The upper tracing is the heart record; the middle is respiration. The large intervals on the time-signal record are ten seconds. *A*, the effect of sticking several times with a sharp needle. *B*, the needle was inserted gently just beneath the epicardium. *C*, weak faradic stimulation of the ventricle after all branches of the vagi were cut except the post-branchial ramus of the fourth branchial division on each side. The hypobranchial and other spinal nerves from the intact portion of the cord were also cut.

reflex movements in the anterior gill region, apparently through the more anterior cranial nerves. It therefore appears that the vagus innervation of the heart, both efferent and afferent, is by way of two pairs of branches, one pair from the post-branchial ramus of the

fourth branchial division, as in *Squalus,* and the other pair from the visceral branch of the vagus.

Cadiat (1879) showed that double vagotomy in *Scyllium* results in an increased rate of the heart. McWilliam (1885) and Kolff (1908) have found the same result in teleosts. The writer found a similar effect (Table I). In some instances cutting one vagus gave a considerable increase in rate which was further augmented when the remaining vagus was cut. The effect is most strikingly seen when the initial rate is low. Such figures have been taken to mean that the vagus normally exerts a tonic influence on the heart. In view of the great ease with which reflex inhibition of the heart occurs in elasmobranchs, as shown by Schoenlein and Willem (1894), Lyon (1926), and Lutz (1929), it is doubtful whether the result of vagotomy under the usual experimental conditions is an indication of the existence of normal vagal tone. In one case the initial rate, some time after exposing the heart, was 30 per minute. After cutting the previously prepared left vagus the rate was 34. Following an hour of experimentation, consisting of producing reflex inhibition by various means, the rate fell to 12. Then cutting the right vagus resulted in an increase to 30. Even gentle blowing on a wound is sufficient to produce a considerable reflex slowing of the heart.

Table I

The effect of vagotomy on the rate of the heart of Scyllium canicula, showing an apparent release from vagal tone.

Before vagotomy *Beats per minute*	After double vagotomy	Before vagotomy *Beats per minute*	After cutting one vagus	After cutting second vagus
30	44	16	33	42
24	40	36	36	38
22	36	26	32	36
18	32	32	32	40
20	34	24	24	38
36	44	39	42	44

Many attempts were made to obtain acceleration of the heart by stimulating the medulla or the cord with the vagi cut and with the gills perfused, but, confirming Bottazzi (1902), no acceleration occurred. The vagus was cut high, or in some cases the medulla itself was destroyed, in order not to interfere with any possible union of sympathetic fibers from the hypobranchial or other roots of spinal nerves with the vagus, although a sympathetic supply from these sources was

considered quite unlikely for morphological reasons. The cord was pithed posterior to the eleventh vertebra and a section three centimeters long was exposed anterior to this vertebra. In *Squalus* this section of the cord (fifth to twelfth vertebra) gives rise to fibers passing to the first sympathetic ganglion, according to Müller and Liljestrand (1918). Faradic stimulation of either the exposed cord or the anterior cut surface of the medulla or mid-brain did not produce acceleration of the heart. Neither did faradic stimulation of the first large sympathetic ganglion accelerate the heart. In this case any possible accelerator pathway from the ganglion to the heart by way of the cardiac ramus of the vagus was not disturbed.

Since there is some evidence that the vagus center normally has a tonic inhibitory effect on the heart, and since a period of acceleration is sometimes seen following a period of inhibition, it was considered that during activity of the cardio-inhibitory center there might be a lowering of tone in the accelerator center. After a period of increased activity of the vagus center its tone, through fatigue, might be lowered and this with the return of the accelerator center to its former condition might account for the acceleration sometimes seen. With the vagi cut and the vagus center active a lowering of accelerator tone would be expected to result in slowing of the heart. To test this a preparation with the medulla and cord to the twelfth vertebra intact was used with the gills perfused. Various means shown previously (Lutz, 1929) to produce marked reflex cardio-inhibition were used, such as faradic stimulation of the central end of the cut vagus or the cut lateral line nerve, vigorous mechanical stimulation of the nasal openings, or pinching the sides of the fish between heavy forceps. The records of the heart rate during such procedures did not show slowing, and consequently it is concluded that no lowering of tone in an accelerator center occurred. This can not be taken as complete proof, however, that no accelerator center exists, but since, in addition, no accelerator fibers have been demonstrated, it points strongly to its absence. Acceleration of the heart sometimes seen after a period of inhibition is probably due to fatigue of the inhibitory center.

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Summary

1. Two branches of the vagus go to the heart of *Scyllium canicula*, each carrying afferent and efferent fibers, one from the post-branchial

ramus of the fourth branchial division (fifth branchial nerve), and the other from the main visceral trunk.

2. No acceleration of the rate of the heart occurred on faradic stimulation of the medulla, spinal cord, or first large sympathetic ganglion with the vagi cut.

3. No slowing of the rate of the heart occurred, due to lowering of tone in an accelerator center, on reflex excitation of the cardio-inhibitory center with the vagi cut.

4. Both morphological and physiological evidence indicate the lack of accelerator fibers to the heart of the elasmobranch.

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